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INTERACTION BETWEEN MOUNTAIN PINE BEETLE AND DYNAMICS OF LODGEPOLE PINE STANDS

p. 1-6

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ABSTRACT

The influences of habitat types, diameter classes, and phloem thickness on beetle populations and the reverse, the influence of beetle populations on stand dynamics, form a coordinated inter-relationship within the lodgepole pine ecosystem. The loss of trees to mountain pine beetles is partly a function of stand structure. Beetle population survival may be dependent upon either food supply or elevation, according to the particular habitat involved. This type of information can be used to estimate the probability of tree loss, risk of infestation, and brood survival.

The mountain pine beetle is a native pest exerting numerous and various effects upon the lodgepole pine ecosystem. Historically, the mountain pine beetle has infested large areas of lodgepole pine; within the Intermountain region, it has depleted these stands by periodically killing the largest, most vigorous trees. One of the primary problems of managing lodgepole pine is this ever-present beetle pressure and recurring mortality. In order to provide the timber manager with alternatives for lodgepole pine, it is first necessary to develop an understanding of the life processes within the beetle population and between the beetle and its host tree.

Our ongoing research of mountain pine beetles in the lodgepole pine ecosystem is to develop knowledge having wide application in bark beetle pest problems. Hopefully, these results, ideas, and principles also can be applied to bark beetle problems within other ecosystems.

The loss of trees to the mountain pine beetle is partly the function of stand structure within different habitat types. Stand tables have been constructed for infested trees. These tables are based on phloem thickness, distribution, and frequency of trees of discrete specific diameters within the different habitat types. From these tables, simulated infestations and also the probability of lodgepole pine survival by prescribed diameters for the period of infestation have been constructed.

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In our studies, beetle populations in lodgepole pine have been sampled to determine biological and behavioral relationships between the beetle and its food, habitat, and associates. Factors measured include (a) crowding during the larval development, (b) attack density of the adults, (c) elevation of infested stands, (d) size and distribution of trees within stands, (e) habitat types, (f) parasites and predators, (g) stand density, (h) egg deposition patterns, (i) phloem (food) thickness, and (j) stand structure. We constructed life tables which we analyzed using a competing risk analysis to determine the probability of death that could be attributed to specific mortality factors or a combination thereof. We are now attempting to develop a method of determining risk of infestation and loss due to mountain pine beetle within lodgepole pine stands.

ECOLOGICAL AND BIOLOGICAL RELATIONSHIPS

There are four general categories of knowledge that relate to the biological processes and ecological associations that exist within the mountain pine beetle (*Dendroctonus ponderosae* Hopk.)-lodgepole pine (*Pinus contorta* Dougl.) complex: (1) habitat types; (2) diameter classes; (3) phloem thickness; and (4) beetle populations.

Habitat Type

Habitat types are considered as reflections of differences in environments; both beetle and lodgepole pines react to a given environment in certain ways. Thus, beetle behavior and lodgepole pine survival rate will differ within different habitat types. Roe and Amman (1970) found this within the three major habitat types within which lodgepole pine grows in the Intermountain area: *Abies lasiocarpa/Vaccinium scoparium* (A/V) contained the least beetle activity--44 percent of the stands were actively infested; *Abies lasiocarpa/Pachistima myrsinites* (A/P) contained the most beetle activity--92 percent of the stands were actively infested; and within *Pseudotsuga menziesii/Calamagrostis rubescens* (P/C), 64 percent of the stands were actively infested. These habitat types generally relate to elevation within the lodgepole pine type of the Intermountain region; i.e., the A/V habitat type exists primarily at elevations above 8,500 feet, the A/P within the elevational zone of 6,500 to 8,500 feet, and the P/C habitat type grows below 6,500 feet. The relation of elevation to habitat type is important when considering the behavior of the beetle within these habitat types.

Amman (1969) found that brood production in bark of a given thickness is inversely related to elevation. Mountain pine beetle brood production is quite low, as is survival of the adult, above 8,000 feet--thus, the greater survival of lodgepole pine above this elevation. Up to 2 years may be required for the beetle to complete its life cycle at these higher elevations. Throughout the elevational zone sample, the survival of lodgepole pine was directly related to the elevation of the stand (Amman, in press). This was true even in the presence of an ample food supply (thick phloem and large diameters) at the higher elevations.

Tree Mortality Within Habitat Type

When a stand of lodgepole pine is attacked by the mountain pine beetle, obviously not all trees are killed. Beetles select the larger diameter trees each year, as well as over the life of an infestation (Cole and Amman 1969). In areas sampled, proportions of trees killed in various diameter classes ranged from 1.1 percent in the 4-inch diameter class to 87.5 percent in the 16-inch and greater class. Correlations between diameters of trees killed and year of kill were highly significant. Larger trees were selected by beetles in early years of the infestation; smaller trees were selected in later years. In these later years, both beetle and infested tree populations were decreasing.



Beetle infestation measured in the Intermountain region rose from approximately 0.5 to 5.0 trees per acre in the early years to a peak of 26 to 31 trees per acre; then declined to 2 to 3.5 trees per acre after most of the larger diameter trees had been killed. The intense period of infestation is usually rather short, lasting approximately 6 years. In our studies, overall tree *survival* has averaged 70 percent for trees 4 inches and greater in diameter.

Large trees produce not only more beetles per unit area of bark but also more per tree because of their greater surface area. Cahill (1960) observed that the height of infestation within a lodgepole pine tree was related to diameter at that height, not to diameter at breast height (d.b.h.). The figures for infestation height by Cahill and our figures on beetle emergence at d.b.h. were used to calculate the populations of beetles produced in trees of different sizes. These figures showed that beetle production could vary from 300 beetles for trees 8 to 9 inches d.b.h. to more than 15,000 for trees 18 inches d.b.h.

We found that 24 beetles per square foot at d.b.h. would be sufficient to infest and kill a tree using the assumption that the infestation rate was 12 female beetles per square foot of bark surface (the rate commonly observed in the field) and a 1:1 sex ratio. Thus, a tree 8 to 9 inches d.b.h. would produce only one-third enough beetles to infest and kill a 12-inch tree. Only infested trees 12 to 13 inches d.b.h. would produce more emerging than attacking beetles. If we assume that one-third to one-half of the beetles that emerge fail to make successful attacks (a conservative assumption), only trees 14 inches or larger d.b.h. would produce enough beetles to increase the infestation or maintain it at the previous year's level.

Relation of Beetle Emergence to Phloem Thickness

Insect population is apparently food-limited within a given area if only trees 14 inches and greater in d.b.h. produce enough beetles to maintain or increase the infestation and if, in fact, the beetle progressively destroys its preferred food supply. Generally speaking, the average thickness of phloem is greater in large than in small trees, and a greater proportion of the large trees is likely to have thick phloem.

Phloem thickness is one of the most important factors affecting mountain pine beetle survival. In our studies, phloem thickness was consistently and by far the strongest independent variable each year; it accounted for up to 62 percent of the variance in numbers of emerging beetles per square foot of bark surface. We found that the significant independent variables are phloem, stand density, and plot elevation for all but 1 percent of 66 percent total variation (Amman 1969).

BROOD SURVIVAL

Depth of phloem in small and large trees is the most obvious difference related to the survival of bark beetle broods. Larvae feed on phloem; thus, Amman (1969) hypothesized that the number of mountain pine beetles completing development within a given area of bark depends on depth of phloem. Although the relation of phloem depth to tree diameter is highly variable, most trees having thick phloem are large in diameter; conversely, trees having thin phloem usually are small in diameter.

The effect of intraspecific competition within mountain pine beetle broods also is related to phloem (food supply) and population density. As the number of inches of egg gallery and, hence, the number of eggs per unit of bark increases, competition among the resulting larvae also increases. Consequently, survival of beetles decreases in a given area of bark, unless phloem depth (quantity) is sufficient to offset the effect of intraspecific competition.

Table 1.--Probability and life expectation of a mountain pine beetle

Stage	Pr_{ij}	$V(Pr_{ij})$	SE	\hat{e}_i	$V(\hat{e}_i)$	SE
Egg	0.776	0.00661	0.0813	114	168.03	12.96
E-2d instar	.222	.01001	.1000	113	134.36	11.59
E-2-4th instar	.197	.01692	.1301	57	69.29	8.33
E-2-4 pupae	.015	.01387	.1178	33	15.50	3.94
E-2-4-P adult	.010	.00769	.0877	15	6.76	2.60

Where the cause of death of an individual is not specific, the probability of an individual mountain pine beetle being alive at any one life stage and the life expectancy (in days) at that stage can be calculated using the competing risks analysis (Cole¹). From our analysis of life tables, most of the events believed to cause critical change in the population occur in the third larval stage--crowding, food shortage, parasites, predators, and spring weather conditions. Such events coincide with the largest probability variation, which occurs in this third instar. The following example of brood survival (table 1) is based on three assumptions: (1) attack density is 12 females per square foot of bark; (2) each female beetle constructs 10 inches of egg gallery and oviposits 5.4 eggs per inch of this gallery; and (3) phloem depth is 0.10 inch. The total egg population for this situation would be 648.

PROJECTION OF CURRENT INFORMATION

The question now arises as to how this information can be combined and used to benefit the timber manager. Previously, most managers were immediately inclined to request chemical control action to halt an infestation of the mountain pine beetle in lodgepole pine. Amman and Baker (1972) compared lodgepole pine stand structures that sustained mountain pine beetle infestations. Some stands had been treated; others had not. Results showed that beetle populations declined in approximately the same number of years in both treated and untreated stands. Survival of lodgepole pine in these two types of stands was comparable with one exception; in two additional stands where the infestation was still active, chemical control had reduced the rate of tree mortality. In such situations, immediate logging of infested stands is recommended.

Roe and Amman (1970) have shown that the probability of infestation varies by habitat type. For example, there is about a 66 percent probability of lodgepole pine surviving to 16 inches d.b.h. in the *Abies lasiocarpa/Vaccinium scoparium* habitat type; but only about a 25 percent probability of surviving to this size in the *Abies lasiocarpa/Pachistima myrsinites* (A/P) type. Cole and Amman (1969) have speculated that beetle population growth is food limited below 8,200 feet in elevation; above this elevation population growth is temperature (weather) limited.² These relationships coincide with habitat types within the lodgepole pine stands in the Intermountain region.

¹Walter E. Cole. Mountain pine beetle dynamics in lodgepole pine forests: an approach and its analysis. Invitational paper given at IUFRO Congr., Gainesville, Fla., March 1971

²Gene D. Amman. The mountain pine beetle--dynamics and role in the lodgepole pine ecosystem. Invitational paper given at the Entomol. Soc. Am. Natl. Meet., Miami, Fla., December 1970.

It is now apparent that beetles select lodgepole pines of the largest diameter and those that usually have the thickest phloem; this upsets the persistent postulate that bark beetles select weakened, decadent trees. In lodgepole pines, trees containing the best growth and vigor (thickest phloem) offer the greatest potential for population buildup of beetles.

A simulation of beetle infestation in a lodgepole pine stand within an A/P habitat type has shown that the beetle can attack the larger diameter residual trees (at an approximate rate of 0.1 or less tree per acre) after an epidemic has run its course. The majority of the population emerging from these residual trees probably attacked the smaller diameter trees. Perhaps a few beetles may attack one or two larger diameter trees that can produce a surplus of beetles; this could sustain the beetle population period. Many relationships remain to be determined in the epidemiology of the mountain pine beetle. Furthermore, the simulated infestation showed that tree losses of epidemic magnitude can occur once the stand has enough trees to support an infestation.

Amman³ has hypothesized that the relationship between associate insect populations and the mountain pine beetle is a primary factor in maintaining the latter population during long endemic periods; Amman is presently studying this relationship. The interdependence of governing factors at low population levels is without a doubt more involved than at a full scale epidemic.

This interaction of beetle with host tree relates to the ecosystem concept. Using this concept, we could project and predict the rise and fall of a mountain pine beetle empire and thus thoroughly evaluate the need for a decision by management. This means that we must possess intimate knowledge and the capability to detect, understand, and then quantify the governing (if not all) ecological processes acting within this dynamic association.

³Gene D. Amman. Personal communication on file at Intermt. For. & Range Exp. Stn., USDA For. Serv., Ogden, Utah.

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